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Harbour seal (Phoca vitulina) abundance within the Firth of Tay and Eden estuary, Scotland: recent trends and extrapolation to extinction

Running head: Rapid harbour seal decline and extrapolation to extinction

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ABSTRACT

1. Aerial surveys have detected alarming declines in the counts of harbour seals in several regions across Scotland.
2. Demographic data and simple models were used to examine the recent decline in the numbers of harbour seals counted in one population within a Special Area of Conservation (SAC) on the east coast of Scotland. The models suggest that the continuation of current trends would result in the species effectively disappearing from this area within the next 20 years.
3. While the cause of the decline is unknown, it must be reducing adult survival because the high rate of decline cannot be wholly accounted for by changes in other demographic parameters.

4. Recovery of the population to the abundance recorded at the time the SAC was designated (2005) is likely to take at least 40 years, even if the cause of the decline is immediately identified and removed.
5. The models suggest that partial removal of the cause can have only limited benefits to population recovery, and there are unlikely to be any long-term benefits from introducing or reintroducing additional individuals while the underlying problem persists. Therefore, if the population of harbour seals in this area is to recover it is essential that the sources of the increased mortality are identified and measures are put in place to manage these.

KEYWORDS: coastal, littoral, monitoring, Special Area of Conservation, conservation evaluation, mammals

INTRODUCTION

The UK is home to around 30% of Europe's harbour seals (*Phoca vitulina*), with the majority of these hauling out at island and coastal sites in the north and west of Scotland (SCOS, 2013). Harbour seals in Scotland have been monitored on an approximately five-yearly cycle since the late 1980s. Two populations, in part of the Moray Firth and around the Firth of Tay, have been surveyed more frequently. The surveys have detected alarming declines in the number of harbour seals observed at haulout sites in several regions. This trend is most apparent in populations in Orkney and on the north and east coasts of Scotland, where numbers have declined by between 65% and 90%, respectively, since the 1990s (Duck and Morris, 2014). Importantly, the decline in number of seals counted is not simply a consequence of changes in seal behaviour altering the proportion of time seals spend hauled out during the moult. A recent telemetry study comparing harbour seals in the declining Orkney population and a stable population on the west coast of Scotland demonstrated that the proportion of animals hauled out during the survey window was high in both areas, and similar to previously published proportions for this species (Lonergan *et al.*, 2013). The declines in harbour seal counts are thus likely to represent real reductions in the numbers of animals present in the region.

Harbour seals are protected under the Marine (Scotland) Act 2010, which prohibits the killing of any seal except under a licence granted by the Scottish Government explicitly for the protection of fisheries or fish farms. There is also the capacity under the Marine (Scotland) Act 2010 to designate seal conservation areas where it is considered necessary to further encourage the proper conservation of seals. Furthermore, a number of harbour seal Special Areas of Conservation (SAC) have been designated under the EU Habitats Directive (for a map of SACs in Scotland, see: http://www.scotland.gov.uk/Publications/2011/03/16182005/54). The Firth of Tay and Eden Estuary (FTEE; Figure 1) was designated an SAC in 2005 in part due to its importance as a breeding and haulout site for harbour seals. Between 1990 and 2002 the average aerial survey count in the FTEE was 640 harbour seals but annual aerial surveys since 2002 indicate a continuing and significant decline in this population: in 2013 only 50 animals were counted within the FTEE (Duck and Morris, 2014).

To address this situation, the ultimate and proximate causes of the decline must be identified. This, in turn, requires a sound understanding of the population structure and its dynamics. For a number of reasons, estimating the structure of pinniped populations is not straightforward (Lonergan, 2014; see discussions in Matthiopoulos *et al.*, 2014). When the population of interest is critically small and in decline minimising disturbance to the population is particularly important, but in addition to aerial surveys, targeted – and repeated – land-based surveillance studies are necessary to estimate key demographic parameters such as adult survival rates, age structure, sex ratio and fecundity (Bowen *et al.*, 2003; Mackey *et al.*, 2008). Some age classes can be identified when observing harbour seals at a distance – for example, very small animals obviously are young and sub-yearlings can be identified by characteristically pale unpatterned pelage (Thompson and Rothery, 1987). Large mature adults may also be distinguishable from other age/sex classes. However, some one-year old animals are similar in length to small adults (Härkönen and Heide-Jørgensen, 1990) and the species is less sexually dimorphic than many other pinnipeds (Burns, 2008). This lack of obvious dimorphism means that visual identification of the sex of adult harbour seals from a distance is seldom possible, so assumptions about sex ratio of survey counts must be adopted. The sex of animals could be determined non-invasively from the DNA analysis of scats left at haulouts, but obtaining a representative sample from the population is difficult and moving from this to estimating the structure of the population is seldom practical. Furthermore, harbour seals can haul out in sex-related groups so haulout groups may not provide an unbiased estimate of sex ratio. Mass mortality events and strandings data can provide information on the sex ratio, age structure and fecundity of affected populations – but with the caveat that these data are likely to be biased towards particular groups of animals (e.g. Härkönen and Heide-Jørgensen, 1990; but see also Härkönen *et al.*, 2007). Relatively unbiased samples may be obtained where animals are part of a subsistence hunt or culled for management purposes but there are no such samples available for harbour seals in the UK. In the absence of direct estimates of these demographic parameters, indirect estimates and information from other similar populations must be adopted.

Here, available demographic information on the Firth of Tay and Eden estuary and neighbouring harbour seal populations is pooled from across multiple sources to characterize and contextualize decadal trends in abundance within the region, to explore the potential proximate causes of the decline and to extrapolate to future population sizes under various scenarios. Insights gained from this exercise are discussed in relation to the future management and conservation of this population specifically, and of harbour seals in the UK more generally. The results confirm a rapid decline in the number of harbour seals hauled out in the FTEE and demonstrate that, if the problem persists at its present rate, the population will become extinct from this area within 20 years.

DATA & ANALYSIS

All analyses were implemented within the R statistical framework (R Development Core Team, 2013) and are based on the number of seals counted at haulouts. These numbers can be converted into rough population estimates by multiplying the counts of harbour seals by a factor of 1.4 (Lonergan *et al.*, 2013) and those of grey seals by a factor of 3 (Lonergan *et al.*, 2011) to allow for those seals not hauled out at the time of the survey.

Harbour seal population in Firth of Tay and Eden Estuary

Aerial surveys during the moulting period are used to monitor the abundance of harbour seals in the UK. Surveys are conducted from either a fixed-wing aircraft using conventional photography or from a helicopter using thermal imaging during the first three weeks of August, in the period two hours before and after low tide (Thompson *et al.*, 2010b). These counts represent an index of the minimum population abundance. Previous research suggests that the proportion of animals hauled out and available to be counted is similar between sites, so persistent interannual changes in the counts are unlikely to be due to changes in seal haulout behaviour (Lonergan *et al.*, 2013).

Counts were made in the FTEE region in most years from 1990 to 2000 and annually from 2002 – 2013 (Table 1). Four previous counts in 1971, 1975 and 1984 were also included in the analysis, although they used a different survey method. These were boat-based survey counts made during the June/July breeding/pupping season and are likely underestimates of the total population size. Thompson and Harwood (1990) counted twice as many seals in Orkney using aerial surveys conducted during the moult period than using boat-based surveys during the breeding/pupping season.

To investigate trends in the harbour seal counts, a generalized additive model (GAM) (Wood, 2006), with quasipoisson errors and a log link function, was fitted to the data by maximum likelihood. As the later part of the trajectory appeared to resemble an exponential decay, a similar generalized linear model (GLM) was also fitted, with different exponential rates of population growth up to 2000 and from 2001 onwards. This initital transition point was chosen visually, and its suitability was checked by fitting models with a range of transition dates. Model suitability was assessed by examining residual dispersion and quasi-Akaike Information Criterion values (QAIC Akaike, 1976; Burnham and Anderson, 2002).

Additional sources of information existed for this population and were included in the assessment of the population trajectory. In 2010, 2011, and 2012 land-based counts of harbour seal pups were conducted in the FTEE during the June/July breeding/pupping season. These numbers, combined with the counts of adults during the August moult, provide an estimate of the proportion of pups in the population. Additionally, since 2008, harbour seal carcasses with distinctive 'spiral' or 'corkscrew' injuries have been found at various locations around the UK, including a total of 36 carcasses within or close to the Firth of Tay and Eden estuary (Table 2). The pathology of these injuries has been described elsewhere (Bexton *et al.*, 2012), and the potential causes were discussed in Onoufrinou *et al.* (2014) and Thompson *et al.* (2015). Recent observations of adult male grey seals predating on harbour seals and grey seal pups have demonstrated that the characteristic 'spiral' lesions can be inflicted by another seal (Thompson *et al.*, 2015; van Neer *et al.*, 2015). The number of such harbour seal carcasses reported in the FTEE is likely to underestimate the total number of animals that are killed in this way because the data describe only animals that wash ashore and are reported. Carcasses of animals that are killed far from the shore are unlikely to wash ashore and will be underrepresented in this dataset. As with all marine mammal strandings data, it is extremely difficult to estimate the scale of under-reporting, but it is likely to be large for pinnipeds. Additionally, the relative buoyancy of animals of different sexes or ages is likely to affect the chance of their carcasses being recovered, and variation in this may make the sample unrepresentative. In the absence of more appropriate data, the sex ratio of these mortalities over the years 2008 to 2013 was investigated by fitting binomial GLMs.

Neighbouring populations

There are a few, small, harbour seal groups neighbouring the FTEE population: in the Firth of Forth (~ 50 km to the south) and the Montrose basin (~50 km to the north) that could be potential sources of immigrants or destinations for emigrants (Figure 1). Until recently, far fewer animals were counted in those areas than in the FTEE. However, that difference is less clear now that the FTEE counts have decreased. Four counts are available from the Firth of Forth (Duck and Morris, 2014), but it is difficult to estimate trends from so few data points. Here, it was assumed that the uncertainty in these counts was similar to those from the FTEE. The counts were modelled using a GAM with quasipoisson error distribution and with the same overdispersion as was estimated from the FTEE data (scale = 13.3). GLMs were also fitted to the data collected after 2000, when the FTEE counts began to show a decline.

Grey seal population in Firth of Tay and Eden Estuary

Harbour seals share the FTEE with larger and more abundant grey seals (*Halichoerus grypus*). The only available information about the number of grey seals in this region comes from August harbour seal moult surveys, when grey seals are also counted. Seventeen counts of grey seals were made between 1990 and 2013 (Table 1), and one count was made during a boat-based survey in 1984. To investigate trends in the count data over this time period, a GAM was fitted with quasipoisson error distribution and a log link function.

RESULTS

Harbour seal abundance in the Firth of Tay and Eden estuary showed positive growth prior to 2001 after which there was a clear transition to a rapid decline. Emigration of seals to nearby haulouts, or local redistribution, could not be ruled out, but seems unlikely based on available counts of neighbouring populations and distances to those populations. Potential proximate causes for the decline are explored in more detail, including changes to haulout behaviour, fecundity, survival and emigration.

Harbour seal population in Firth of Tay and Eden Estuary

The choice of the year 2000 as the transition point in the population trajectory was supported by the fact that models fitted with transitions in 1998, 1999, 2001 and 2002 had greater residual overdispersion. Equivalent models fitted with Poisson errors also had higher AIC values than the model with a break point at year 2000. The results of the GAM and the GLM with a change in trajectory after 2000 were similar (Figure 2), especially for recent years. While the truth is probably somewhere between these extremes, a model where two exponential trajectories were fitted along with a shrinkage spline allowed the two representations to compete and produced results indistinguishable from the original GLM. A similar model containing two smooth functions and two exponential trajectories, all meeting between 2000 and 2001, produced identical results. These combined models therefore support a relatively sudden transition between two periods with different, but stable, rates of exponential population change.

The population growth rate between 1970 and 2000 was estimated at 4.6% *p.a.* (95% Confidence Interval 3.5 - 5.7). This lies within the range of values that have been observed in other harbour seal populations (Thompson *et al.*, 2005; Lonergan *et al.*, 2007), but is still far from the 12% instrinic rate of increase for harbour seals (Härkönen *et al.*, 2002). The different methodology used for the early surveys may limit their comparability with the later ones, and the reliance that can be put on the estimate of population growth prior to 2000. However, even if count data from the three years of boat-based surveys were doubled (following Thompson and Harwood, 1990), estimated population growth was still positive (1.8% *p.a.*; 95% CI 0.9 - 2.8). This source of uncertainty does not affect the estimated annual rate of decline since 2000, which was 19.9% (95% CI: 16.8 – 23.0). This is significantly faster than the estimated annual rate of decline in the harbour seal population around the Orkney Islands and northern Scotland (13% *p.a.*; 95% CI 10.8 - 14.8), another area where there are serious concerns for this species (Lonergan *et al.*, 2013). Detailed examination of the modelled trajectories showed that some recent counts (2009, 2011, 2013) and GAM predictions lie below the trajectory estimated by the GLM (Figure 2), suggesting that the decline of the FTEE population is unlikely to be slowing.

A total of 12 harbour seal pups were observed during onshore visual searches of the FTEE in 2010, 6 in 2011, and just one in 2012 (R. Milne, SMRU, *pers. comm.*). In those years 124, 77 and 88 adult harbour seals were observed during the moult aerial surveys, meaning roughly 1 pup was observed for every 10 animals counted in 2010 and the ratio was 1:13 in 2011, and 1:88 in 2012. These ratios are lower than those estimated for other populations. For example, in The Wash (~450 km south of the FTEE on the east coast of England) the ratio of peak pup numbers observed via aerial surveys during the breeding season to mean total moult counts of adult animals was much higher (1:1.6 to 1:3.5; SCOS, 2012). The low proportion of pups in the area in recent years implies either a lower fecundity among adult females or that a smaller proportion of the population are adult females.

The sex ratio of the unusual mortality events caused by spiral lesions (based on recovered stranded carcasses) was modelled with bionomial GLMs. If it is assumed that there were no detection biases on the basis of sex, GLMs suggested that 29% (95% CI: 16 – 47) of the animals killed in this way were male. An intercept-only model performed worse than one including a year covariate (ΔAIC = 5) providing some evidence to suggest the proportion had changed over the period. Unfortunately, it is not possible to test whether the carcasses match the sex ratio of the surviving population, or other populations under more normal conditions.

Neighbouring populations

GAMs fitted to the four available counts from the Firth of Forth (116 in 1997; 280 in 2005; 148 in 2007; and 145 in 2013) showed no evidence of changes in abundance over the period. A GLM fitted to the data from after 2000 (n = 3), when the FTEE counts were declining, suggested the population in the Firth of Forth may have been in decline but the annual rate of change was in the range -0.21 to +0.05 (95% CI). The range in the FTEE during the same period was -0.23 to -0.16. The uncertainty associated with small samples in the Firth of Forth means that approximately 45 more surveys would be required to match the precision of the current estimate of the trend in the FTEE. Without this added precision, no firm conclusions can be made about trends in abundance in the Firth of Forth area.

Over the last ten years, 36 harbour seals have been fitted with telemetry tags in and around the FTEE. Inspection of their GPS tracks showed two of them hauled out at or beyond Montrose to the north, and another two hauled out within the Firth of Forth to the south. Other individuals swam beyond these places without coming ashore there(Sparling *et al.*, 2012). It therefore seems unlikely that the abundance trajectories in these areas will be wholly independent.

Grey seal population in Firth of Tay and Eden Estuary

Fitting a GAM to the counts of grey seals in the FTEE in August showed that there has probably been a slow decline (~1% *p.a.*) in their numbers over the period since 1990 (Figure 3). While this change is not statistically significant (95% CI: -4.3 – +0.9), it clearly shows that, at least in August, there has not been a substantial increase in grey seal numbers in the FTEE. Grey seal pup production has been increasing at around 9%

p.a. in the British North Sea breeding colonies (SCOS, 2013); though pup production at the Isle of May (a SAC for grey seals), a breeding colony about 35km from the FTEE harbour seal population, has been fairly stable (Duck and Morris, 2011). Grey seal and harbour seal at-sea and haulout usage overlaps in the FTEE (Jones *et al.*, 2013) but the observed stability in the number of grey seals in the area implies that any competitive pressure they apply to the harbour seals is unlikely to have increased, unless there is a total carrying capacity for pinnipeds in the area that has steadily reduced over this period. Reductions in pinniped carrying capacity could be caused by a reduced prey resources, or reductions in access to suitable haulout locations. The latter is not the case as there are ample suitable haulout locations for both species in the FTEE; the former is less easily determined. North Sea regime shifts (Beaugrand, 2004; Beaugrand *et al.*, 2014) and trends in pelagic fish communities (e.g. Shephard *et al.*, 2014) are well documented but the impact of these changes on marine mammal diet and condition is not well understood.

Potential proximate causes

There is one behavioural change, and four changes in the population's demographics, with the potential to produce the observed decline in harbour seal numbers in the FTEE. It is unlikely that a single factor is responsible for the dramatic decline in this population, but for the sake of clarity, each is discussed in isolation below.

The counts of hauled out animals could decrease if haulout behaviour changed and the proportion of time animals spent out of the water during the survey window declined. Harbour seals tagged in the FTEE in 2001-2003 did not show significant interannual variation in haulout probability, but because seals lose their tags during the moult, no animals were tracked during August, when the counts used in the present study were made (Sharples *et al.*, 2009). However, a recent study in Orkney, where the harbour seal population is also declining rapidly, used flipper-attached satellite tags to track animals throughout their moulting period. The animals showed similar haulout behaviour to that previously reported elsewhere and to a control sample of individuals from a stable population on the west coast of Scotland (Lonergan *et al.*, 2013). Furthermore, to account for the magnitude of the reductions found in the FTEE population since 2000, a

93% reduction in the proportion of time spent hauled out around daytime low tides during the moult (and hence proportion of animals available to be counted) would be required. The number of harbour seals hauled out peaks during their moult (Watts, 1996; Thompson *et al.*, 2005), so whilst interannual shifts in haulout behaviour are possible, it is considered unlikely that they were the main cause of the observed changes.

The decline could be caused by a reduction in pup and/or adult survival. If all pups die, populations decline at a rate determined by the mortality rates among adults. There are few adult survival estimates for harbour seals in the region. In the Kattegat-Skagerrak, the annual survival rate of male harbour seals has been estimated at 0.91, while female survival was slightly higher (Härkönen and Heide-Jørgensen, 1990). A higher rate 0.97 (95% CI 0.92 – 0.99) was estimated in the Cromarty Firth, in northeastern Scotland, from photo identification mark-recapture of live animals (Mackey *et al.*, 2008); and in a nearby population, recent estimates were 0.95 (95% CI 0.91-0.97) for females and 0.92 (95% CI 0.83-0.96) for males (Cordes and Thompson, 2014). The FTEE population is therefore declining too rapidly for even a total failure in recruitment to provide a complete explanation, though it could be a contributory factor. If adult female survival is assumed to have been 0.92 before the decline, then a total failure of recruitment would need to have been accompanied by a reduction in adult survival of at least 10% to produce the observed changes.

The decline could simply be explained by a reduction in overall survival. Lower adult survival would increase the proportion of juveniles in the population, and result in a drop in the ratio of pup numbers to total abundance and an accelerating rate of decline in abundance. A gradual decrease in the proportion of females in the population would have similar effects. The female-bias in the recovered spiral-cut carcasses is difficult to interpret due to incomplete information on the cause of the mortalities and potential detection biases (e.g. due to differences in carcass buoyancy between sexes). However, the low pup to adult ratio found in the population in recent years is consistent with changes in the population structure and a shift towards fewer females than males. The counts and GAM trajectory falling below the predicted values from the GLM in recent years (Figure 2) hint at an accelerating rate of decline, but as such provide very limited evidence to support such a conclusion.

The same argument that applies to pup/adult survival also means that reduced fecundity alone cannot entirely explain the decline. While reduced fecundity could contribute to the observed low pup to adult ratio, if fecundity were zero (which it cannot be given the observations of pups in 2010, 2011, and 2012) the adult mortality would have to equal the observed rate of decline, i.e. 19% *p.a.* An increase in the age at first reproduction would be equivalent to a reduction in fecundity, but again, there are no data available to test this hypothesis.

Emigration and immigration are the last demographic parameters that must be examined. Emigration is only distinct from mortality if the animals arrive somewhere else. The Moray Firth contains the only harbour seal population in reasonable proximity that is sufficiently large that an immigration of tens of animals per year could possibly pass unnoticed (Duck and Morris, 2014). Emigration from the FTEE to smaller populations south of the Moray Firth or to the Firth of Forth would likely have been detected as substantial percentage increases in survey counts. A cessation of immigration to the FTEE population from neighbouring populations could possibly have contributed to the observed decline, but there is no evidence that the FTEE population received large numbers of immigrants in the years before the decline occurred. The Moray Firth population is again the most likely source of animals for such redistribution but it is > 250 km away from the FTEE and telemetry data suggests that harbour seal redistribution at this scale is likely to be minimal (Thompson *et al.*, 1994; Cunningham *et al.*, 2009; Sharples *et al.*, 2009). While net immigration to the FTEE population in years prior to 2000 is possible, it is considered that reduced immigration is unlikely to explain the observed rapid population decline since 2000.

Future scenarios

Attempts to predict the future trajectory of the FTEE population depend on assumptions about the underlying cause of the decline and any potential mitigation. This section attempts to project the future of the FTEE population under various possible scenarios.

'Business as usual'

If no management actions are taken to identify and rectify the cause of decline in this population, and if it continues at the rate established since 2000 (19% *p.a.*), effective population extinction is likely. Even ignoring stochastic effects, this can be expected to occur before 2040 (Figure 4). In practice, random variations in the sex ratio of births and timings of deaths are likely to make this occur much sooner.

A simple stochastic model of the female component of the FTEE harbour seal population assuming 92% annual survival of non-pups (Mackey *et al.*, 2008), 40% survival of pups (Harding *et al.*, 2005), 90% of females older than 3 years old pup each year (Härkönen and Heide-Jørgensen, 1990) and a 50:50 sex ratio, produces a population growth rate of 5% *p.a*. Introducing an additional 25% mortality, affecting adults and non-pup juveniles, changes this to an 19% *p.a.* decline. Treating each birth and each individual's annual mortality risk as an independent draw from binomial distributions, and starting with a population of 35 non-pup females, suggests extinction is likely to occur after 20 years (95% CI, from 1000 replicates: 12 – 34 yrs). Figure 5 shows the trajectories of 100 replicate simulated populations. The starting population size of 35 animals was chosen on the assumption that more than half of the 50 animals counted in 2013 were female, but that some of those were pups. This starting estimate may be slightly low to account for the proportion of animals missed from the moult count because they were in the water, but the model also neglects the counteracting possibility that extinction occurs as a result of all males dying or that individual deaths are not independent.

Source of decline eliminated

The GLM model fitted to survey counts after 2000 suggested that the 2013 survey was one where a low proportion of animals were hauled out, and that 70 animals could have been expected to be seen, rather than the 50 animals that were actually observed. Using a scaling factor of 1.4 to account for those animals not hauled out during the survey window (Lonergan *et al.*, 2013) the total population abundance was estimated to be 100 animals. With this – perhaps over optimisitic – number, and assuming the sex-ratio and age structure are stable and comparable to those for other harbour seal populations, and ignoring stochastic effects such as elimination of males, the time for abundance to return to 600 can be estimated. Table 3 contains some estimated recovery times based on different population growth rates. The additional years needed for population recovery per year of delay in eliminating the present cause of decline are also presented.

The population growth rates explored in Table 3 were chosen on the basis of existing empirical information on harbour seal population dynamics within the North Sea region. Twelve percent is the present growth rate for the Wadden Sea harbour seal population (TSEG, 2013) and is often considered to be around the maximum sustainable growth rate for pinniped populations (Härkönen *et al.*, 2002). This represents the most 'optimistic' scenario whereby the cause of the present situation is immediately resolved and the population reaches and maintains a maximum growth rate for at least 16 years. Perhaps more realistic are the projections from growth rates between 3% and 6%. The population in The Wash was growing at 3% *p.a.* prior to the 1988 phocine distemper epidemic. It then increased and was approximately 6% *p.a.* between the 1988 and 2002 epidemics (Thompson *et al.*, 2005; Lonergan *et al.*, 2007). If the abundance estimates that were made for the Tay in the 1970s are believed to be consistent with the more recent ones, then this population was growing at around 4.5% *p.a.* up to the beginning of the recent decline. In these scenarios, the FTEE population could be expected to recover to its previous abundance in 30 – 60 years. Even in this 'ideal' scenario, there is no 'quick fix'. In reality, the different survey method used in early counts was likely to have caused underestimation of abundances and therefore overestimation of the rate of population growth. Assuming that the underestimation was about half (Thompson and Harwood, 1990), this has the effect of decreasing the population's rate of growth prior to 2000 to about 2%.

Source of decline partially eliminated

The accepted "normal" maximum growth rate for pinniped population is 12% *p.a* (Härkönen *et al.*, 2002), but the FTEE population is declining by around 19% *p.a.* The impact of the problem is thus 31% (i.e. 12% - -19%= 31%); a halving of the impact of the problem to 15.5% could be expected to result in a population rate of decline of 3.5%

p.a. (i.e. -19% + 15.5% = -3.5%). Whatever is affecting this population would therefore need to be reduced by more than half of the total impact for the population to stabilize at its current level, and by more than that to permit it to begin to recover. A growth rate of 6% under optimal conditions similar to that observed in The Wash (Thompson *et al.*, 2005; Lonergan *et al.*, 2007), would imply that population recovery would require at least ¾ of the problem to be resolved. If the maximum achievable growth rate were 3% *p.a.* – which may be more representative of Scottish harbour seal populations – then recovery would depend on finding an almost complete solution to the problem.

Female shortage in recovering population

Direct measurement of the true sex ratio in the FTEE population is neither feasible, nor advisable given its present state and the need to minimize disturbance. A project is underway to estimate the sex ratio of this population non-invasively via DNA testing of scats; however, recovery of suitable samples has proven difficult in this region. Additionally, the method requires many assumptions about patterns of haulout behaviour and defecation and is unlikely to produce an estimate of sex ratio that is truly representative of the population. However, if there is a shortage of females in the recovering population, this would both increase the risk of local extinction because of stochastic variation (i.e. all the females dying) and slow the initial stages of the recovery. Populations starting with more highly skewed sex ratios would initially grow more slowly and it would take longer for their growth rates to recover to more normal values.

Extinction & recolonization

Though capable of long distance movement, harbour seals generally exhibit high site fidelity, generally using haulouts less than ~25 km apart (Thompson *et al.*, 1998; Cunningham *et al.*, 2009; Sharples *et al.*, 2012; Cordes and Thompson, 2015), and there is evidence that genetic diversity increases with distance (Stanley *et al.*, 1996; Goodman, 1998). Philopatry could thus limit their ability to recover from local extinctions. There is no indication that males and females of this species travel together (Thompson *et al.*, 1998), therefore the establishment of a population would seem to require multiple colonizing events.

There are two examples of UK harbour seal populations that became extinct and have recovered to some extent, in the Tees and the Ythan Estuaries. The population in the Ythan was removed by shooting in 1979 and 1980. It is not known when the first animals returned, but by the mid 1990s harbour seals were seen regularly in the estuary. The harbour seal population in the Tees disappeared at an unknown date in the mid 19th century when large parts of the estuary were developed (Woods, 2012). Harbour seals recolonized the Tees Estuary in the 1970s or early 1980s and the population has grown slowly to reach around 20 to 50 seals (Woods, 2012). The first successful pupping was recorded in 1994. The more rapid recolonization of the Ythan Estuary may be related to the proximity of small harbour seal haulout groups on the coast 45km to the north (Figure 1). In contrast, the nearest groups to the Tees are in the Firth of Forth, 200km to the north, or in the River Humber, 170km to the south (Figure 1).

In the event of harbour seal extinction in the Firth of Tay and Eden Estuary, the most likely source of colonizing animals would be the small populations in the Firth of Forth, 50 to 60 km away, or the animals that haul out north of Montrose, about 40km from the FTEE haulouts. However, it is not clear that these groups of animals actually are sufficiently separated to follow different population trajectories. Telemetry tags attached to harbour seals in the FTEE have recorded some of these individuals hauling out in the Firth of Forth and around Montrose (SMRU, *unpublished data*). Beyond these areas, and the few animals now on the Ythan Estury, the next nearest potential sources of immigrants to the FTEE would be the Moray Firth or the Tees and Humber Estuaries (Figure 1). These areas are > 200km away, so reestablishment of the FTEE population would be unlikely to occur rapidly.

DISCUSSION

The data available to assess the extent of, and potential mechanisms for, the decline in harbour seal numbers in the Firth of Tay and Eden Estuary are diffuse and often sparse. Nevertheless, analysis of these limited data provides insights into the potential proximate causes for the rapid decline. Furthermore, they provide an avenue to explore possible scenarios for the future of this population and the likely impact of specific management policies. Such an approach may also be useful in other studies of populations where demographic data are limited or non-existent.

Using such data, the present study demonstrates that if the trends identified here continue at the present rate, harbour seals are likely to effectively disappear from the FTEE within the next 20 years. Exploration of the demographic parameters that could produce such changes indicate that the, presently unidentified, cause of the decline must be reducing adult survival (potentially in addition to reducing fecundity and/or pup survival). Simple projections and simulations demonstrate that, if the cause is immediately identified and removed, recovery of the population to the abundance when the SAC was designated is likely to take at least 40 years and that partial removal of the problem would have limited benefits. Thus there are unlikely to be any long-term benefits from introducing or reintroducing additional individuals while the problem persists.

Globally, harbour seals are classified as a species of 'least concern' on the IUCN Red List; however, the rapid population declines such as the one described here and in Orkney and Shetland (Thompson *et al.*, 2001; Lonergan *et al.*, 2007, 2013) represent significant regional losses of a large and iconic predator. In the FTEE population, a reduction in overall survival must be invoked to account for the rate of decline – but the potential causes of an increase in mortality are various and often inter-linked.

Substantial declines in food availability or accessibility could increase competition for limited resources between conspecifics, and with grey seals. Harbour seals tagged in the area foraged primarily in an area ~ 25-100 km from the haulout site (Sharples *et al.*, 2009, 2012), but there are few simultaneous telemetry data to assess whether grey seals actively exclude harbour seals from some areas. Given that there is a high degree of dietary overlap between the species and that both use the FTEE to haul out, there is considerable potential for overlap in foraging areas. If inter-specific competition is indeed hastening the demise of the FTEE harbour seal population, the question of any relevant management action remains. However, a reduction in harbour seal condition as a result of increased competition for resources would most likely be manifest in the population as reduced fecundity and/or pup survival. In addition to natural mortality from predators, this has been proposed as an explanation for the decline of the harbour seal population on Sable Island, Canada (Bowen *et al.*, 2003). Reduced fecundity and/or pup survival could be a factor in the decline of the FTEE population but neither of these can wholly account for the rapid rate of decline observed A substantial reduction in adult survival must also be invoked.

A notable recent phenomenon has been the discovery of multiple carcasses with 'corkscrew' or 'spiral' injuries on the east coast of Scotland and England (Thompson *et al.*, 2010a; Bexton *et al.*, 2012). The majority of these have been adult female harbour seals, or juvenile male grey seals. The pathology of these characteristic injuries is consistent with the animals being pulled through a ducted propeller (Bexton *et al.*, 2012), but there now exists unequivocal evidence that such injuries can be, and in some cases are being, inflicted by adult male grey seals (Thompson *et al.*, 2015; van Neer *et al.*, 2015). Investigations into the prevalence of this behaviour and its impact on harbour seal populations are ongoing. While the numbers of 'corkscrew' harbour seals recorded in the FTEE since 2008 are fairly low (n = 36), these are likely to underestimate total numbers because not all carcasses will be washed ashore, detected, or reported. Furthermore, the 6 corkscrew mortalities reported in 2013 represent >10% of the total number of animals counted at the FTEE that year. Clearly, mortality at this rate is not sustainable for this population.

Each year of delay in addressing the cause of the decline seems likely to both increase the risk of local extinction and further delay any recovery to historical abundances by several years. Future management actions should be focused on unequivocally identifying and ameliorating this, and other, potential sources of additional harbour seal mortality if the population is to be conserved.

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710 **TABLES**

711 **Table 1:** Counts of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*)
712 hauled out during the annual moult in August in the Firth of Tay and Eden Estuary
713 Special Area of Conservation since regular surveys began. Prior to 1990, counts were
714 made from boat-based surveys conducted during the breeding season (June/July). From
715 1990, counts were made from a fixed wing aircraft using standard photography, from a
716 helicopter using thermal imaging, or using both of these methods ('both').

Year	Harbour seals	Grey seals	Survey method
1971	296		boat
1971	170		boat
1975	208		boat
1984	310	259	boat
1990	467	912	fixed wing
1991	670	1549	fixed wing
1992	773	1226	fixed wing
1994	575	1468	fixed wing
1997	633	1891	thermal imaging
2000	700	2253	fixed wing
2002	668	1593	fixed wing
2003	461	1663	fixed wing
2004	459		fixed wing
2005	335	843	both
2006	342	1379	fixed wing
2007	275	1559	both
2008	222	508	fixed wing
2009	111	450	fixed wing
2010	124	1555	fixed wing
2011	77	1322	fixed wing
2012	88	1202	fixed wing
2013	50	482	thermal imaging

717

718 **Table 2:** Occurrence and sex of harbour seal (*Phoca vitulina*) mortalities from
719 corkscrew injuries recorded on the east coast of Scotland south of Aberdeen.

	Male	Female	Unidentified
2008*		2	
2009*	1	3	
2010		8	1
2011	1	5	3
2012	4	2	
2013	3	2	1

720 * Likely under-reporting of corkscrew strandings in these years

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724

Table 3: The number of years required for a population to increase from 100 to 600 individuals, at various annual growth rates. The final column is the number of additional years required to balance out the present population decline continuing at 19% for one additional year.

Annual growth rate	Approximate recovery time	Additional years per year of delay
3%	60	7
4.5%	40	5
6%	30	4
12%	16	2

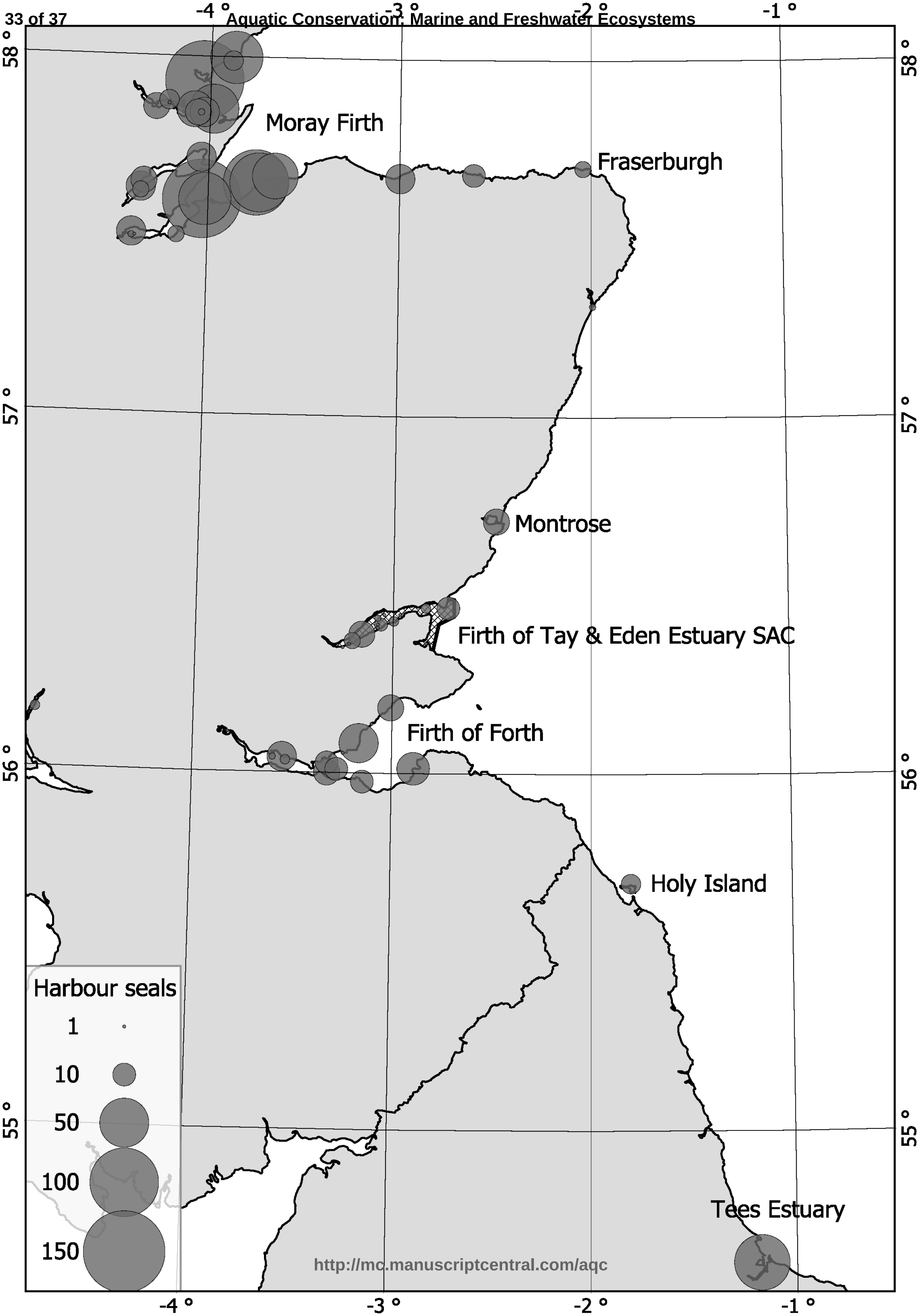
Figure 1: Map of northeast England and eastern Scotland showing the location of the Firth of Tay & Eden estuary (FTEE) Special Area of Conservation (SAC) and neighbouring harbour seal population sites. Harbour seals counts from 2013 are presented.

Figure 2: Numbers of harbour seals counted during surveys of the Firth of Tay and Eden Estuary. Solid circles indicate aerial surveys that were carried out during the annual moult in August. The hollow squares indicate an earlier boat-based survey method that counted animals hauled out during the breeding season in June/July, and therefore may not be truly comparable to counts post-1990. The solid line is an estimated trajectory from a GLM where the rate of exponential population growth changed after 2000. The dark shaded region around it shows the associated 95% confidence intervals. The dashed curve (and 95% confidence interval) is the result of a GAM that assumes changes in the population growth rate changed smoothly over the period.

Figure 3: Numbers of grey seals counted during summer surveys of the Firth of Tay and Eden Estuary Special Area of Conservation. Solid circles indicate aerial surveys that were carried out during the annual harbour seal moult in August. The hollow square indicates an earlier boat-based survey method that counted animals hauled out during the harbour seal breeding season in June/July, and therefore may not be truly comparable to counts post-1990. The dashed line is an estimated trajectory from a GAM, and shows a steady exponential decline. The shaded region around the trajectory shows the associated 95% confidence intervals.

Figure 4: Projection of the GLM model (and 95% confidence intervals) of the harbour seal counts in the Firth of Tay and Eden estuary shown in the red shaded region after 2013.

Figure 5: Simulated trajectories for the decline of the Firth of Tay and Eden estuary harbour seal population. Each line shows the numbers of females aged at least 1. Populations that appear to recover from zero abundance are those that were reduced to contain only juveniles. By neglecting the possibility of extinction through total loss of males, this model is likely to overstate the length of time this population will survive.


Moray Firth
Fraserburgh
Montrose
Firth of Tay & Eden Estuary SAC
Firth of Forth
Holy Island
Tees Estuary
Harbour seals
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10
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100
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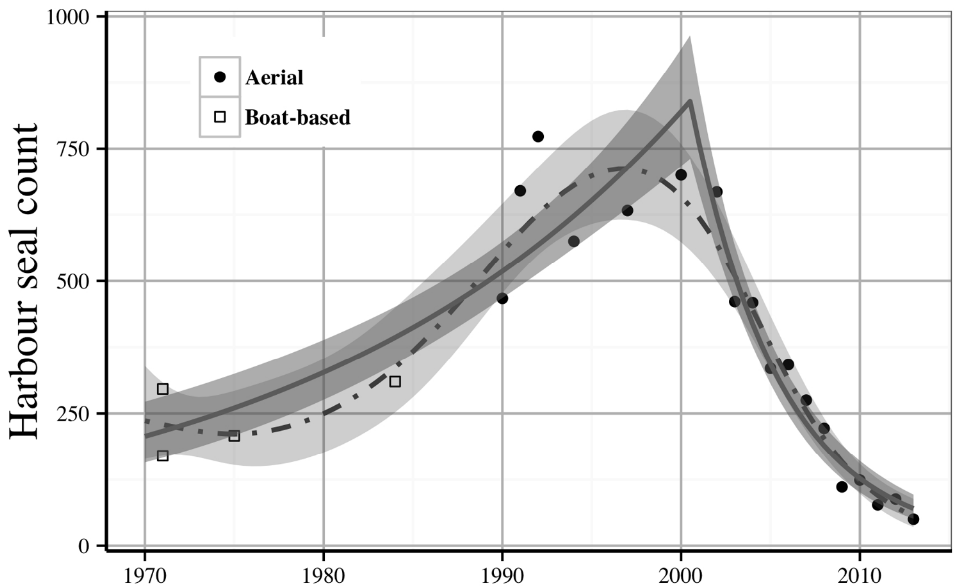
-4 °
-3 °
-2 °
-1 °
58 °
57 °
56 °
55 °



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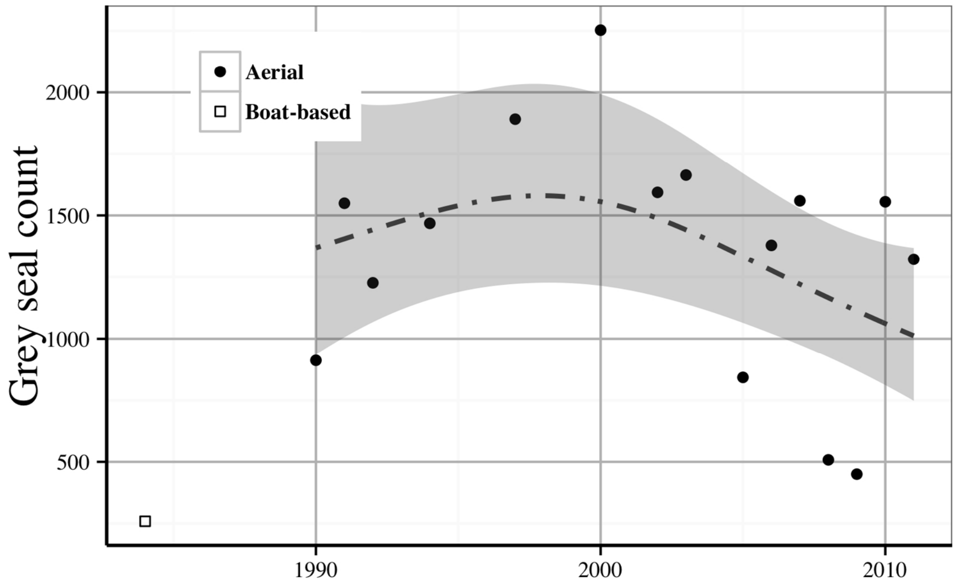

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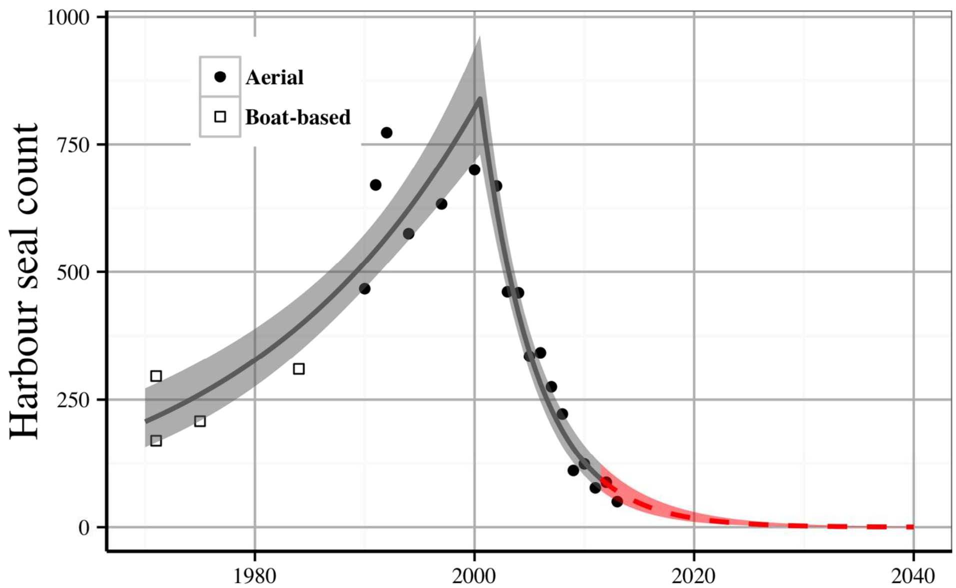

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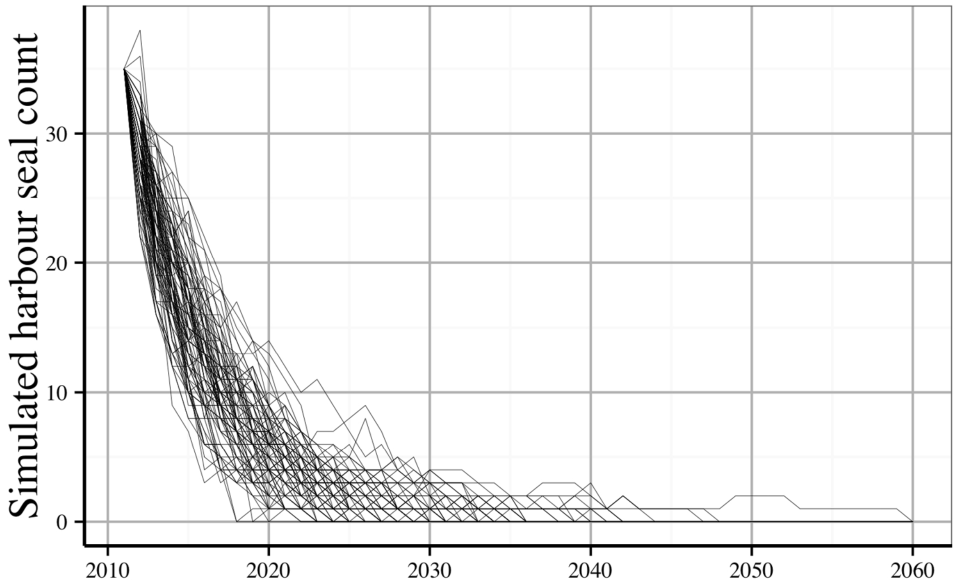

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